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Research Article

Food fight: *Gammarus tigrinus* demonstrate competitive advantage over native *G. duebeni*

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Abstract

Introductions of non-native species (NNS) are major drivers of biodiversity loss. Gammarids (Crustacea, Gammaroidea) have been particularly successful in establishing and spreading in their non-native range, especially in Europe. While their impacts are wide-ranging, interference competition with native species has received limited study to date. Here, we assessed the competitive abilities of the successful North American NNS *Gammarus tigrinus* relative to the European native *Gammarus duebeni*, over a chironomid larva as a single food resource. We staged four types of dyadic contest encounters, with individuals of the native or NNS added to the experimental arena containing the food resource, and inter- or intraspecific competitor individuals added upon the first individual taking possession of the resource, or after 20 minutes. *Gammarus tigrinus* were more likely to take hold of the bloodworm in the opening 20 minutes, and did so more quickly than *G. duebeni.* During this period, they were also less thigmotactic than the native, being more explorative and spending a smaller proportion of time in the outer zone of the arena. They exhibited more aggressive interactions and activity with increasing size and mass, whereas larger *G. duebeni* were shown to be less aggressive and less active. *Gammarus tigrinus* were found to be significantly less likely to lose possession to *G. duebeni* than they were to conspecifics, whereas *G. duebeni* were similarly likely to lose possession to *G. tigrinus* as to conspecifics. Overall, our findings indicate that the behaviour and competitive ability of *G. tigrinus* demonstrated here add to a list of traits that facilitate its invasion success. In addition, our method offers potential as an effective, standardisable means of assessing the competitive abilities of gammarid NNS. We encourage future studies to develop it further, incorporating alternative resources, such as habitat, and to assess the role of ecologically relevant abiotic stressors in determining contest outcomes.

Key words: Animal behaviour, Baltic Sea, contests, exploitative competition, impact assessment, interference competition, non-native species

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Introduction

Global translocations of non-native species (NNS) are major drivers of biodiversity loss, affecting ecosystem services, human health and welfare, food security, and economic costs (Pyšek et al. 2020, Cuthbert et al. 2021, IPBES 2023). Amphipod crustaceans of the family Gammaroidea are one group of particularly damaging NNS, which have been highly successful at displacing natives, especially in Europe (Grabowski et al. 2007, Cuthbert et al. 2020). Gammarids are significant drivers of disturbance through competition for food and habitat resources, as well as predation, with major implications for native biodiversity in recipient freshwater and brackish ecosystems (Conlan, 1994). One such example is the North American *Gammarus tigrinus*, which has been shown to have negative impacts on native amphipod assemblages in introduced ecosystems (Jänes et al. 2015, Reisalu et al. 2016), as well as socio-economic costs to fishermen through damaged fishing gear and injured catches (Pinkster et al. 1977). Native to the brackish waters of tidal estuaries along North America's Atlantic coast, the first European occurrence was in England in 1931, likely arriving in ship ballast water (Sexton and Cooper 1939). From here, it was introduced to Northern Ireland in the 1950s before spreading southwards, replacing the native *G. lacustris* and *G. duebeni celticus* as the dominant gammarid in Lough Conn's sublittoral zone (O'Grady and Holmes 1983). It arrived and established in mainland Europe when the English stock was deliberately introduced to the polluted Werra river in Germany in 1957, and subsequently when the Lough Neagh population was introduced to IJsselmeer in the Netherlands in 1964. Since then, its spread has led to cases of replacement or population decreases for the native *G. pulex*, *G. zaddachi* and *G. d. duebeni* (Nijssen and Stock 1966, Pinkster et al. 1992, Kazanavičiūtė et al. 2024). In 1975, it reached the German part of the Baltic Sea, and from there its coastal range expansion has continued (see Rewicz et al. 2019 and references therein).

The Baltic Sea is the world's largest brackish-water basin and a highly unique ecosystem, with a low number of native species, many of which are postglacial immigrants, and at least 132 non-native and cryptogenic species (Casties et al. 2016, Ojaveer et al. 2017). Here, the combination of few native species, environmental instability and high anthropogenic pressure means the ecosystem is deemed sensitive to biological invasions (Reisalu et al. 2016, Rewicz et al. 2019). Indeed, *G. tigrinus* is joined by another North American gammarid NNS in *Melita nitida*, as well as Lake Baikal's *Gmelinoides fasciatus*, and seven NNS from the Ponto-Caspian region: *Chaetogammarus warpachowskyi*, *Chelicorophium curvispinum*, *Dikerogammarus villosus*, *D. haemobaphes*, *Chaetogammarus ischnus* (formerly *Echinogammarus ischnus*: Copilaș-Ciocianu et al. 2023), *Spirogammarus major* (formerly *E. trichiatus*: Copilaș-Ciocianu et al. 2023), *Obesogammarus crassus*, and *Pontogammarus robustoides* (Rewicz et al. 2019). Of these, *G. tigrinus* is viewed as one of the most euryhaline (Grabowski et al. 2006). While various studies have looked at the environmental tolerance of the species (Casties et al. 2019, Paiva et al. 2020), its life history traits (Pinkster et al. 1977, Grabowski et al. 2007) and even its ability to facilitate the consumption of congeneric native species by predators (Kotta et al. 2010), there remains a gap in the literature with regards to interference and exploitative competition outcomes over food resources with native gammarids. More broadly, there has been little study of contests to understand interspecific interactions, and its role on niche partitioning, species coexistence and biodiversity (Paijmans and Wong 2017), with even less in an invasion ecology context (but see, for example, Zeng et al. 2019).

Heeding recent calls for more studies to help decipher the competitive mechanisms at play between NNS and native species (Damas-Moreira et al. 2020), we paired *G. tigrinus* with *G. duebeni*, which has been outnumbered or replaced by the NNS in Ireland, the Netherlands and in the Baltic Sea (e.g. Vistula Lagoon, Poland: Grabowski et al. 2006; Dassower See, Germany: Kazanavičiūtė et al. 2024). Staging a series of dyadic contest experiments over a finite food resource, we used an experimental setup that involved staging four types of contest pairings: *G. tigrinus* vs *G. tigrinus*, *G. duebeni* vs *G. duebeni*, *G. tigrinus* vs *G. duebeni* and *G. duebeni* vs *G. tigrinus*. We sought to investigate species behaviour and determine the role of species identity, as well as body size and mass (traditional proxies for fighting ability, termed "resource holding potential": Arnott and Elwood 2009) in determining contest outcomes. Specifically, we assessed boldness, activity and competitive ability using eight key tests. Boldness was assessed by examining the latency to approach the resource (1) and thigmotactic behaviour (2). Next, we assessed activity via the number of line crosses (see Fig. 1) per time in the experimental arenas (3), and finally, we assessed competitive ability (4–8). Boldness, i.e. how individuals behave in potentially risky situations (Réale et al. 2007), has been suggested to be a determinant of whether individuals are likely to disperse or remain sedentary, or whether they are short or long-distance dispersers (Fraser et al. 2001). This, alongside activity, has been highlighted as a beneficial behavioural trait across multiple stages of the introduction process (Chapple and Wong 2016), and they have been positively correlated in a number of invasive NNS (Brodin and Drotz 2014, Lukas et al. 2021). With *G. duebeni* having no known non-native populations (Paiva et al. 2018, Cuthbert et al. 2020), we propose these traits will be less obvious for the native species. As a result, we hypothesised that: (1) expecting it to be bolder, the non-native *G. tigrinus* is more likely than the native *G. duebeni* to take hold of the food resource in the opening 20 minutes, and of the individuals from both species taking hold of the food resource during that period, *G. tigrinus* is faster to take possession of the resource; (2) for the period of time that the individual added first is alone in the arena, *G. tigrinus* is less thigmotactic, i.e. spends less time in the outer ring of the arena; and (3) *G. tigrinus* is more active than *G. duebeni*. In terms of their competitive ability over food resources, our hypotheses were informed by previous studies which have shown *G. tigrinus* to be

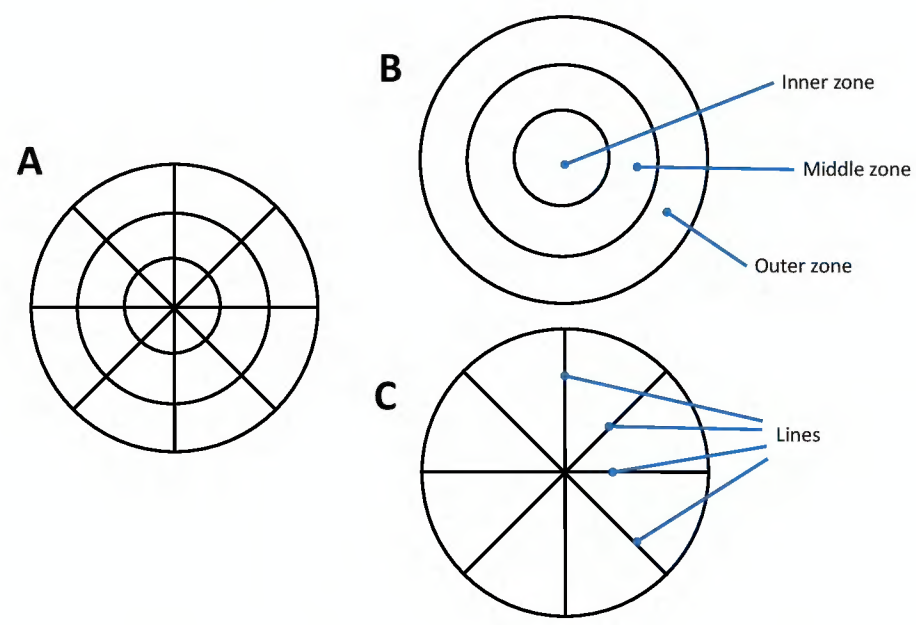

Figure 1. A diagram of markings on the experimental arena, broken down into the constituent zones (**B**) and lines (**C**). The zones were used as a determinant of thigmotactic behaviour (hypothesis 2), whereas the lines were used to determine line crosses, a measure of activity (hypothesis 3).

Table 1. Ethogram showing recorded behaviours and how they were defined by the researchers.

Behaviour category	Behaviour	Definition
Aggression	Bump	Collision between the two gammarids
	Approach	Approach of gammarid out of possession towards bloodworm held by other gammarid
	Wrestle	Both gammarids holding same bloodworm
Boldness	Outer zone	Gammarid in outer ring (Fig. 1)
	Middle zone	Gammarid in middle ring (Fig. 1)
	Inner zone	Gammarid in central ring, also initial location of bloodworm (Fig. 1)
Activity	Line cross	When gammarid crosses from one "segment" into another (Fig. 1)
Possession	In possession	Gammarid holding bloodworm
	Not in possession	Gammarid not holding bloodworm

successful at outcompeting native species for preferred habitat (Kotta et al. 2011, Reisalu et al. 2016), while exhibiting high feeding rates (Dick 1996, Dickey et al. 2021) and demonstrating aggression towards native gammarids (Orav-Kotta et al. 2009, Kotta et al. 2010). As a result, we hypothesise that: 4) the trial type (i.e. species match-up) and size disparity will have significant effects on the number of aggressive interactions (i.e. bumps, approaches: see Table 1); 5) contests involving the "aggressive" *G. tigrinus* will be more likely to escalate into "wrestles" over the food resource 6) the number and duration of wrestling bouts will be significantly affected by trial type and contestant size disparity; 7) for the gammarid added first, larger *G. tigrinus* will spend greater proportions of time in possession; and 8) *Gammarus tigrinus* will be more likely to dispossess *G. duebeni*, and larger individuals will be more likely to dispossess smaller individuals.

Methods

Gammarid collection and maintenance

Both *G. tigrinus* and *G. duebeni* were collected from Travemünde, Germany (53°83'N, 10°64'E) in August 2017 and kept in laboratory conditions (temperature: 16 °C, light regime: 12 h:12 h). While the prevalence of these species from this locality were approximately 50:50 in 2017, the NNS has since become dominant and the native extirpated (Briski, pers. obs.). Stocks of both study species were held in constantly aerated 56 L glass aquaria, filled with 10 ppt, 5-µm filtered Kiel Fjord water. Sand and artificial structures in the form of ceramic tubes were added to the tanks to simulate natural habitats. The animals were fed *ad libitum* with a mixture of commercial crustacean food (Tetra Mix, Tetra Crusta, and Dr. Shrimp Healthy).

Contest trials

48 hours before trials began, study gammarids were taken from holding tanks and held individually in 100 ml of 10ppt water within plastic dishes (8.4 cm diameter, 4.2 cm height) containing two ceramic tubes for shelter. Study individuals of length 5.9 mm and upwards from both species were chosen, and randomly assigned to dyads for contests. To standardise hunger levels, and in turn motivation, gammarids were given 3 defrosted frozen *Daphnia* sp. (Vivantis Aqua, Germany) for one hour, after which any remaining *Daphnia* were removed by pipette. They were then starved for the following 47 hours. After the removal of food, all individuals were measured

and weighed within 30 minutes, so as to give ample recovery time prior to trials. For this, individuals were blotted dry and weighed, and photographed next to a ruler for scale. Using ImageJ software (Schneider et al. 2012), the head-to-telson length of each individual was measured (see Table 2 for means and standard errors, SE, and Suppl. material 1 for the size and mass measurements for each study individual).

Table 2. Mean head-to-telson lengths and masses for contestants of both species over the four experimental trial types.

Matchup	Species	Mean length (mm)	Length SE	Mean mass (g)	Mass SE
1	1. *G. duebeni*	8.356	0.600	0.051	0.006
	2. *G. duebeni*	7.912	0.399	0.043	0.006
2	1. *G. duebeni*	9.097	0.514	0.066	0.010
	2. *G. tigrinus*	8.519	0.522	0.048	0.006
3	1. *G. tigrinus*	8.958	0.339	0.061	0.006
	2. *G. duebeni*	8.189	0.478	0.048	0.005
4	1. *G. tigrinus*	8.630	0.263	0.057	0.006
	2. *G. tigrinus*	8.489	0.330	0.051	0.006

Trials were run in September 2022. Prior to trials commencing, a single defrosted frozen chironomid larva (i.e., bloodworm; Vivantis Aqua, Germany) was added to the experimental arena (same dimensions as plastic dishes mentioned above; design shown in Fig. 1). Each trial had a "first" and "second" gammarid, referring to the order in which they were added. Video recording commenced (CX Action Camera, ACTIVEON Inc., U.S.A.) and the first gammarid was added to the arena five minutes after the addition of the bloodworm. The second gammarid was added as soon as the first gammarid took hold of the bloodworm or, in the case where the first gammarid did not take hold of the bloodworm, after it had been in the arena for 20 minutes (mean +/- SE time until addition of second gammarid: 14.675 +/- 1.692 seconds). Trials ended twenty minutes after the addition of the second gammarid. There were four trial types (n = 9 contests per trial type, mean and SE lengths and masses of contestants outlined as per Table 2) designed to assess both intraspecific (essentially control trials) and interspecific competition as follows: 1) *G. duebeni* (first gammarid) v *G. duebeni* (second gammarid); 2) *G. tigrinus* (first) v *G. tigrinus* (second); 3) *G. duebeni* (first) v *G. tigrinus* (second); and 4) *G. tigrinus* (first) v *G. duebeni* (second).

Video analysis was conducted using BORIS v7.4.14 (Friard and Gamba 2016), with the coded behaviours falling under the categories of "aggression", "activity", "boldness", and "possession" (definitions outlined as per Table 1).

Hypotheses and statistical analyses

We tested eight hypotheses, using the following statistical analyses:

1. To determine if, of the individuals that took possession, there was a difference between the two species in latency to take possession of the resource, the effect of species on latency to approach was assessed by Wilcoxon rank sum test.
2. To assess whether, of the individuals added first to the arena, there was a difference between the species in terms of thigmotactic behaviour for the period of time that they were the sole individual in the arena, we used beta regression.

The proportion of time in the outer zone (Fig. 1) was used as the dependent variable, with species and 1) head-to-telson length, or 2) mass, used as the independent variables. Dispersion was allowed to depend on the effect of species (see Cribari-Neto and Zeileis 2010).

3. To determine if there was a difference in activity between the species, we used generalised linear models (GLMs) assuming Quasipoisson error structures to account for over-dispersed data, with the number of line crosses per time spent in the arena used as the dependent variable, and focal species, opponent species and either 1) head-to-telson length, or 2) mass, used as the independent variables. Individuals added first and individuals added second were pooled for this analysis.
4. To assess the role of trial type (i.e. species match-up) and size disparity - using 1) head-to-telson length disparity or 2) mass disparity - on the number of aggressive interactions (i.e. bumps, approaches: see Table 1), we used a Quasipoisson GLM, again due to over-dispersed count data.
5. To determine if there was a significant effect of match-up on the likelihood of wrestling occurring during a contest, a 4-sample test for equality of proportions without continuity correction was used.
6. To determine if the duration of wrestling bouts was significantly affected by trial type and contestant size disparity, using either 1) head-to-telson length disparity or 2) mass disparity, on the time spent wrestling, a linear model was used. To determine the effect of trial type and size disparity on the number of wrestling bouts, we used a Quasipoisson GLM due to over-dispersed count data.
7. To test if larger *G. tigrinus*, of the gammarids added first, spent greater proportions of time in possession, we used a Quasibinomial family GLM with time in possession of the gammarid added first as the dependent variable and the trial type and 1) head-to-telson length disparity or 2) mass disparity used as the independent variables.
8. To determine if *G. tigrinus* were more likely to dispossess *G. duebeni*, and if larger individuals were more likely to dispossess smaller individuals, we used binomial GLMs with logit link functions with takeover success when *G. tigrinus* or *G. duebeni* were in possession as the dependent variable, and the species out of possession, and the 1) head-to-telson length disparity or 2) mass disparity, as the independent variables.

Statistical analyses were conducted using R v4.0.3 (R Development Core Team), with graphs created using the 'ggplot2' (Wickham 2016), 'ggpubr' (Kassambara 2023) and 'interactions' (Long 2024) packages.

Results

Gammarus tigrinus were more likely to take hold of the bloodworm in the opening 20 minutes, and those that did, did so more quickly than *G. duebeni* (hypothesis 1). Twenty-one of the individuals added first took hold of the bloodworm in the opening 20 minutes, the majority of which were *G. tigrinus* (*G. tigrinus*: n = 15, 71.4%; *G. duebeni*: n = 6, 28.6%). Of the individuals that took the bloodworm in the opening 20 minutes, *G. tigrinus* had a significantly lower latency (mean +/- SE: *G. tigrinus* 270.00 +/- 55.00 seconds; *G. duebeni* 343.23 +/- 77.36 seconds; Wilcoxon rank sum exact test: W = 74, p = 0.023).

There was a significant effect of species on the proportion of time spent in the outer zone (hypothesis 2), with *G. tigrinus* spending more time in the middle and inner zones than the native *G. duebeni* (Beta regression: z = 5.858, p < 0.001; Fig. 2; Suppl. material 1: table S1). There was also a significant two-way interaction of species and length on activity ($F_{1,67}$ = 5.914, p = 0.019; Suppl. material 1: table S2) as measured by the number of line crosses per time spent in the arena (hypothesis 3), with *G. tigrinus* more active with increasing length, but *G. duebeni* less active with increasing length (Fig. 3A). A similar pattern was shown when mass was accounted for, with a significant two-way species and mass interaction on activity ($F_{1,67}$ = 6.646, p = 0.016; Fig. 3B; Suppl. material 1: table S3).

With regards to hypothesis 4, there was no significant effect of trial type and head-to-telson length disparity or mass disparity on the combined number of bumps and approaches between the participant gammarids (Quasipoisson GLM: trial type the sole independent variable in both minimum adequate models, p = 0.249). However, at an individual level, a significant two-way interaction effect between species and mass on the number of approaches and bumps (Quasipoisson GLM: $F_{1,68}$ = 5.202, p = 0.040; Suppl. material 1: table S4), with larger *G. tigrinus* committing more bumps and approaches, but larger *G. duebeni* committing fewer (Fig. 4).

There was no significant effect of trial type on proportion of contests that led to wrestles (4-sample test for equality of proportions without continuity correction: p = 0.517; hypothesis 5). Similarly, there were no significant effects for trial type and head-to-telson length disparity (Gaussian GLM: length disparity the sole independent variable in minimum adequate model, p = 0.165) or mass disparity

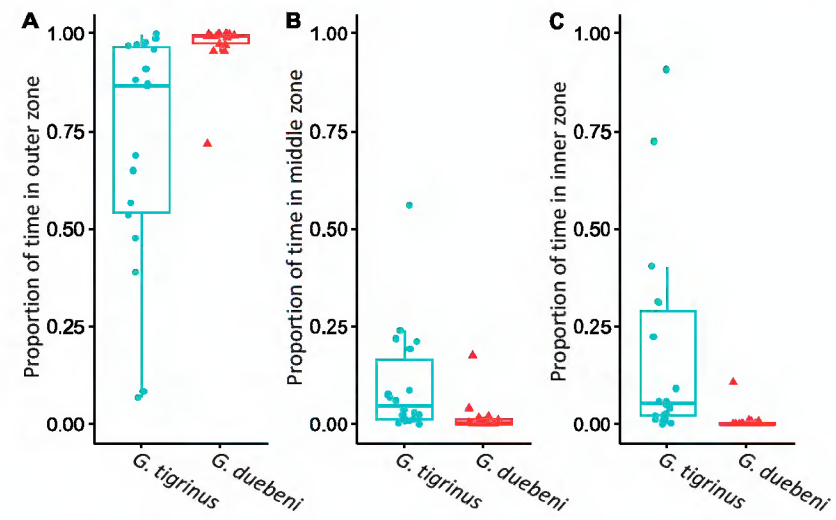

Figure 2. Boxplots outlining the relative proportional time spent in each of the three zones and how this differed between *G. tigrinus* and *G. duebeni* **A** outer zone **B** middle zone **C** inner zone.

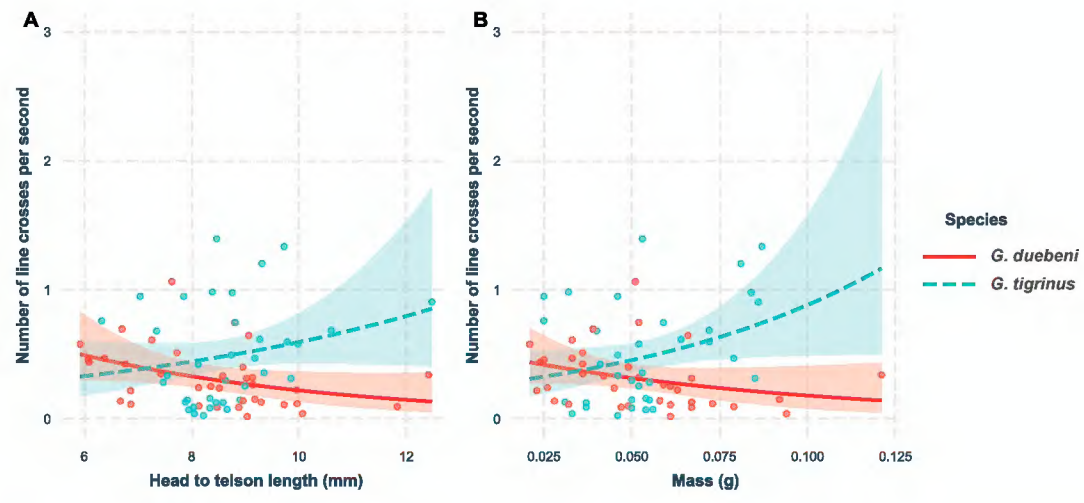

Figure 3. Scatter plots showing the effects of **A** mass and **B** head-to-telson length on the number of line crosses per second in the arena, and how this differed between *G. tigrinus* and *G. duebeni*. Lines shown with 95% confidence intervals.

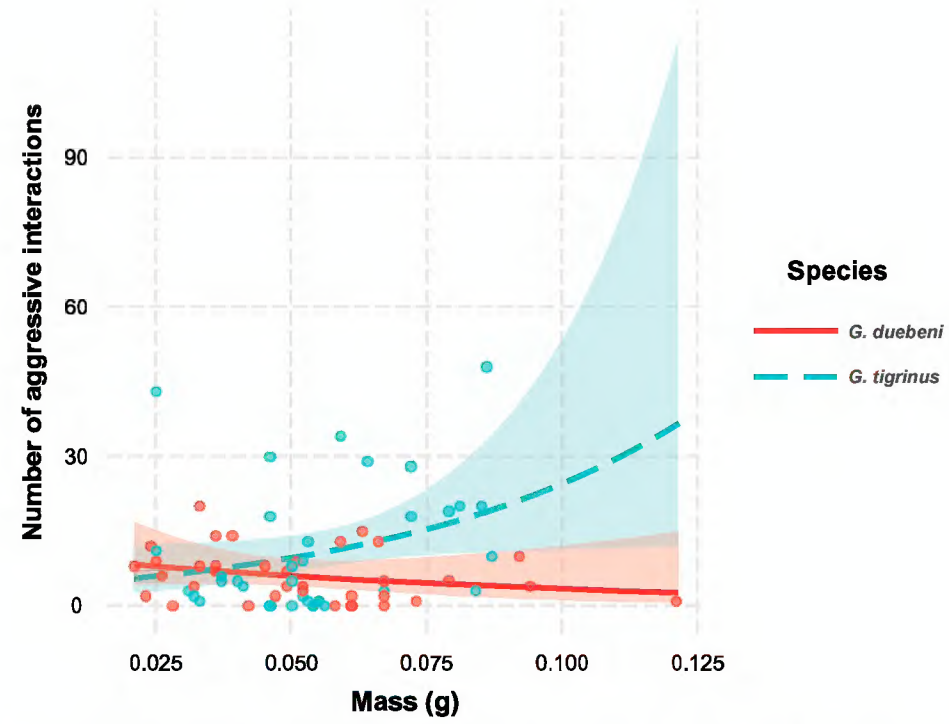

Figure 4. Scatterplot outlining the effect of mass on the number of aggressive interactions, and how this differed between *G. tigrinus* and *G. duebeni*. Lines shown with 95% confidence intervals.

(Gaussian GLM: trial type the sole independent variable in minimum adequate model, p = 0.153) on the log-transformed time spent wrestling or the number of wrestling bouts (Quasipoisson GLM: trial type the sole independent variable in both minimum adequate models, p = 0.115; hypothesis 6).

There were no significant effects of trial type and size disparity or mass disparity on the proportion of time in possession found for the gammarid added first (Quasibinomial GLM: trial type the sole independent variable in both minimum adequate models, p = 0.230; hypothesis 7). However, takeover success when *G. tigrinus* was in possession was significantly affected by the species out of possession (Binomial GLM: z = 2.249, p = 0.025; Suppl. material 1: table S5), with *G. tigrinus* taking possession significantly more than *G. duebeni* (Table 3; hypothesis 8). Takeover success when *G. duebeni* was in possession was not significantly affected by the species out of possession (Binomial GLM: the species previously not in possession was the sole independent variable in minimum adequate model, p = 0.205).

Table 3. Takeover attempt success based on species attempting takeover and species in possession at the time.

Species in possession	Opponent attempting takeover			
	G. tigrinus		*G. duebeni*	
	Successful	Unsuccessful	Successful	Unsuccessful
G. tigrinus	4	1	1	8
G. duebeni	2	2	2	5

Discussion

The introductions of NNS with overlapping ecological niches and functional similarity can lead to displacement of native species, something that has repeatedly been documented for those faced with the arrival of *G. tigrinus* (Pinkster et al. 1992, Jänes et al. 2015, Reisalu et al. 2016). In this study, we staged dyadic contests, using four combinations featuring the NNS and the native *G. duebeni*, over a single food resource, whereby one contestant was allowed up to twenty minutes to take possession of the resource undisturbed, with a second contestant added once the first contestant took possession, or after twenty minutes had elapsed. We found *G. tigrinus* to exhibit

behaviours deemed to be beneficial across multiple stages of the invasion process and to exert a competitive advantage over the native gammarid which, through limiting access to resources, could affect population growth and survival.

During the initial period, we found *G. tigrinus* to be more likely to take possession of the resource, and of the individuals from both species that took possession, *G. tigrinus* exhibited a lower latency to do so than *G. duebeni*. The ability to efficiently identify, locate, take and retain possession of food resources is a valuable way of overcoming competitors in a novel ecosystem. Lower latencies to commence foraging have also been linked to greater boldness (Short and Petren 2008), and indeed, during this same period (i.e. before the addition of the second individual), *G. tigrinus* spent a lower proportion of time in the outer zone, indicating less centrophobic or thigmotactic behaviour than the native *G. duebeni*. Thigmotactic behaviour is a common indicator of where an individual falls along a boldness-shyness axis (dos Santos et al. 2023, Augustyniak et al. 2024), and boldness is a trait offering benefits at different stages of the introduction process. While some behaviours can have mixed effects depending on the stage (e.g. exploratory behaviour might enhance the likelihood of uptake into transport vectors but increase the likelihood of detection by biosecurity checks during transit: Chapple et al. 2011), boldness is thought to provide benefits during uptake, introduction, establishment and spread (Chapple et al. 2012, Gruber et al. 2018). Boldness is also often correlated with other "dispersal-enhancing traits" (Gruber et al. 2018, McGlade et al. 2022) such as activity and aggression within a behavioural syndrome (Sih et al. 2004), and the combination of high boldness and activity levels has been shown to enhance feeding opportunities (Brownscombe and Fox 2013) and survival in the presence of predators (Blake et al. 2018). We also discovered size-dependent activity and aggression differences between the species, with larger *G. tigrinus* found to be more active and aggressive, but larger *G. duebeni* found to be less so. While this aggression did not equate to increased success of dispossessing the native *G. duebeni*, which were equally likely to concede possession to conspecifics as they were to *G. tigrinus*, it may have offered some sort of deterrent, with *G. tigrinus* being better at resisting takeover attempts from *G. duebeni* than from other *G. tigrinus* individuals.

The inability of *G. duebeni* to dispossess *G. tigrinus* when in possession could be explained by competitive naiveté, something that remains relatively unstudied (Heavener et al. 2014). It may be that *G. duebeni* adapt to *G. tigrinus* as a competitor over time, but this is hard to predict, with some behavioural changes instant, some occurring over an individual's lifetime, and some over multiple generations (Ruland and Jeschke 2020). Furthermore, considering the rates at which native gammarids have been replaced by *G. tigrinus* (e.g. Kazanavičiūtė et al. 2024), such adaptive processes may be too lengthy. For example, Heavener et al. (2014) showed that despite a close taxonomic relationship, native bush rats (*Rattus fuscipes*) failed to recognise the chemical cues of non-native black rats (*Rattus rattus*) in Australia, despite the two species interacting competitively for over 200 years. However, adaptation periods can be much shorter. The NNS American mink (*Neovison vison*) established in the UK at a time that otters (*Lutra lutra*) and polecats (*Mustela putorius*), both native competitors, were largely absent. Since then, populations of the native species have recovered and expanded, and mink have changed from being nocturnal to diurnal over the course of a decade, which is theorised as an adaptation to the rebounding natives (Harrington et al. 2009). It remains to be

seen if *G. duebeni* can adapt competitively and quickly enough, or whether they can expand the niche differentiation with *G. tigrinus* through resource partitioning or avoidance, either in space or time.

In the present study, we did not see any significant effect of body mass or length on contest outcome or aggressive behaviour between *G. tigrinus* and *G. duebeni*. Those size measures are commonly used determinants of competitive ability or "resource holding potential" (Arnott and Elwood 2009, Zeng et al. 2019), and would be expected to influence contest dynamics. It could be that the size disparities and sample sizes between our competing species might have been too small to find such an effect, and it is an area that warrants further investigation in future studies. During contests, individuals are thought to assess their own and their opponent's resource holding potential as well as the value of the contested resource, and this can dictate whether individuals risk injurious and potentially deadly fights (Arnott and Elwood 2008). In addition to morphological adaptations, which we propose are less relevant for gammarids, it may be that some species attach a naturally higher value to a contested resource than others, potentially driven by metabolism, or having more specialist demands in terms of diet or habitat. Other studies have also found species to be the most important predictor, rather than size. For example, this was shown for sympatric salamanders (Anthony et al. , 1997) and rockpool fishes (Paijmans and Wong 2017).

While the purpose of this study was to assess species-level differences, the methods employed could also be used to compare the competitive abilities of age-groups, sexes or populations. Indeed, there have been a number of calls to assess population-level differences within invasion ecology of late (Haubrock et al. 2024) and such differences have been noted in our study species. For example, individuals from the Dutch, Lough Neagh-originating *G. tigrinus* population are deemed less adapted to freshwater conditions than those from the German, England-originating population which subsequently invaded the eastern areas of the Netherlands (Pinkster et al. 1992). Therefore, applying dyadic contests across a salinity spectrum could reveal the environmental tipping point where one population is at a competitive advantage. Another avenue for study could be to look at the North American native range of *G. tigrinus*, where it is represented by six genetically distinct lineages grouped in two main clades (the "northern species" and "southern species": Kelly et al. 2006). With the European populations descended from the "northern species" (Rewicz et al. 2019), it would be of interest to see how these clades compare, and whether differences in behaviour make one clade more prior-adapted to exert potential impacts. More generally, such a population focus can allow our method to help test invasion ecology hypotheses like the invasion front hypothesis (Lopez et al. 2012, Iacarella et al. 2015) or anthropogenically induced adaptation to invade (Hufbauer et al. 2012, Briski et al. 2018).

An important next step is to ground-truth the methods applied in this study and to use more real-world examples. While size seemed to play a minor role in our study, we note that adult *G. duebeni* can reach almost twice the size of adult *G. tigrinus* (Kolding 1981, Ward 1985, Grabowski et al. 2007), and we recommend that future studies account for larger individuals to determine their competitive performance and if the trend of decreasing activity and aggression holds. While size disparity can lead to different habitat utilisation and in turn segregation and coexistence (e.g. Platvoet et al. 2009), there are many case studies where much larger gammarid NNS have displaced smaller natives (however, conversely, native

G. lacustris has been displaced by the physically smaller *G. fasciatus* in Lake Peipsi in Estonia and Russia: Panov et al. 2000, Panov and Berezina 2002). One such example is the larger Ponto-Caspian NNS *D. villosus* (adult males can reach 30 mm body length: Nesemann et al. 1995), which has had negative impacts on *G. tigrinus* and *G. duebeni* populations in the Netherlands (Dick and Platvoet 2000). Size disparity may also heighten the risk of contests descending into intraguild predation (Polis et al. 1989), and asymmetrical mutual predation has been shown to be a key driver of NNS replacing natives (Dick and Platvoet 1996, Nakata and Goshima 2006). Staging dyadic contests with large interspecific size disparities could help reveal the prevalence of this phenomenon.

Going forward, we propose that the findings of this study, and the methods implemented to derive them, offer applied potential in the form of NNS impact assessment. Indeed, recent impact assessment measures comparing resource consumption rates between NNS and trophically analogous natives have become incredibly popular within invasion ecology (Dick et al. 2014, Faria et al. 2023, 2025). Nevertheless, the *per capita* nature of the method, with study individuals left to feed in the absence of conspecific or interspecific competitors (Dickey et al. 2022), is an obvious shortcoming that could be addressed using the method at hand. Indeed, while the functional response-derived Relative Impact Potential metric (Dick et al. 2017, Dickey et al. 2020) has incorporated proxies for the numerical response to compare the population impacts of NNS relative to native species, it could be further developed to include a measure of competitive ability (or conversely, the degree of biotic resistance posed by native species within an ecosystem: Twardochleb et al. 2012, MacNeil et al. 2013), leading to a measure of potential impact across three axes. This would determine: 1) the "undisturbed" maximum feeding rate relative to a native, 2) the potential population size or reproductive rate of a NNS relative to a native, and 3) a measure of interspecific competitive strength to determine the probability of the two prior axes being realised. All three measures will likely change depending on abiotic conditions (e.g. salinity, temperature, noise pollution), and these can in turn be accounted for, allowing, for example, the prediction of future impacts with climate change. These three axes would account for many of the myriad mechanisms and traits that have been suggested as explaining the invasion success and impacts of *G. tigrinus* to date. For example, the NNS exhibits a broad reproduction period, known to be reproductively active all year round in the Gulf of Riga (Kotta et al. 2010), as well as a high reproduction rate, a short development time, high feeding rates with a propensity for "surplus killing" of prey (Dickey et al. 2021), and broad ecological tolerances in terms of salinity, temperature, and pollution (Grabowski et al. 2007, Reisalu et al. 2016).

In summary, we propose that this method, used here to demonstrate the competitive ability of a widespread NNS that has led to population declines of native gammarids across Europe and is expanding its range further (Rewicz et al. 2019), can offer a standardised, effective means of assessing inter- and intraspecific contests over limited resources. Bridging the gap between animal behaviour studies and applied NNS impact assessment, we propose it can be easily tailored depending on the hypotheses and study systems in question. While more ground-truthing is required, we believe it has the potential to become a useful component of horizon scans, and thus facilitate the impact assessment, prediction, and prioritisation of NNS as required by EU legislation and global biodiversity targets.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

JWED and GA conceived the study. JWED conducted the experiments. JWED and JWZ performed the video analyses and conducted statistical analyses. EB and JMJ provided resources. JWED led the writing of the manuscript, with all authors contributing to its development.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Supplementary information

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Data type: docx

Explanation note: **table S1.** Estimated regression parameters, standard errors, *z* values and *p*-values for the Beta regression. The proportion of time spent in the outer zone was used as the dependent variable, with species and 1) head-to-telson length, or 2) mass, initially used as the independent variables, however the minimum adequate model was left with only species remaining following stepwise deletion. Dispersion was allowed to depend on the effect of species. **table S2.** Estimated regression parameters, standard errors, *t* values and *p*-values for quasipoisson generalized linear model. The number of line crosses per time in arena was used as the dependent variable and species of the focal individual, species of its competitor, and head-to-telson length were used as the independent variables. **table S3.** Estimated regression parameters, standard errors, *t* values and *p*-values for quasipoisson generalized linear model. The number of line crosses per time in arena was used as the dependent variable, and species of the focal individual, species of its competitor and mass were used as the independent variables. **table S4.** Estimated regression parameters, standard errors, *t* values and *p*-values for quasipoisson generalized linear model. The number of aggressive interactions (i.e. bumps, approaches: see Table 1) was used as the dependent variable, with species and mass used as independent variables. **table S5.** Estimated regression parameters, standard errors, *z* values and *p*-values for binomial generalized linear model with logit link. Takeover success when *G. tigrinus* were in possession was used as the dependent variable, with the species out of possession, and the 1) head-to-telson length disparity or 2) mass disparity, used as the independent variables. After stepwise removal of terms, the species out of possession was left as the sole independent variable in the minimum adequate mode.

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Supplementary material 2

Gammarid contest data

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Data type: xlsx

Explanation note: Behaviour data, coded using BORIS.

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